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Applied Mathematics Letters 20 (2007) 702–706
Applied Mathematics Letters
www.elsevier.com/locate/aml

A delayed marine bacteriophage infection model☆

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Received 15 October 2004; received in revised form 6 June 2006; accepted 28 June 2006

Abstract

A marine bacteriophage infections model with stage structure is studied. Necessary and sufficient conditions for the extinction and permanence of the system are obtained, which enrich and improve the corresponding results given by S.A. Gourley and Y. Kuang [A delay reaction–diffusion model of the spread of bacteriophage infection, SIAM J. Appl. Math. 65 (2005) 550–566].

Keywords: Marine bacteriophage infection; Delay; Stage structure; Necessary and sufficient conditions; Permanence

1. The model

Dynamics of marine bacteriophage infections have received much attention and many excellent results have been obtained: In [3], Beretta and Kuang proposed a mathematical model for the marine bacteriophage infection and analyzed its essential mathematical features. Later, they [4] extended the model of [3] in modeling of the latent period by suitable delay terms modeling. Recently, Gourley and Kuang [7] considered the following marine bacteriophage infection model with stage structure:

$$\begin{cases} \dfrac{\mathrm{d}S(t)}{\mathrm{d}t} = \alpha S(t)\left(1 - \dfrac{S(t)}{\gamma}\right) - KS(t)P(t), \\ \dfrac{\mathrm{d}P(t)}{\mathrm{d}t} = -\mu_p P(t) - mP^2(t) - KS(t)P(t) + bKS(t-T)P(t-T)\mathrm{e}^{-\mu_i T}, \end{cases} \tag{1.1}$$

where $S(t)$ is the density (i.e. number of bacteria per liter) of susceptible bacteria, $P(t)$ is the density (number of viruses per liter) of viruses (phages). T is a constant and denotes the latency time. The initial conditions for (1.1) are

$$\begin{cases} S(s) = S^0(s) \geq 0, \quad s \in [-T, 0], \text{ with } S^0(0) > 0, \\ P(s) = P^0(s) \geq 0, \quad s \in [-T, 0], \text{ with } P^0(0) > 0, \end{cases} \tag{1.2}$$

☆ This work is supported by the National Natural Science Foundation of China (No. 10371127, No. 10601042, No. 60603028 and KLMM0605).
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0893-9659/$ - see front matter
doi:10.1016/j.aml.2006.06.017

where S^0 and P^0 are prescribed continuous functions. In [7], Gourley and Kuang studied system (1.1) with (1.2) and the existence with a reaction–diffusion version of (1.1). For system (1.1) with (1.2), they obtained the following sharp result on the extinction of viruses $P(t)$:

Theorem 1 (*Gourley and Kuang, [7], Theorem 1*). *Assume*

$$be^{-\mu_i T} \leq 1 + \frac{\mu_p}{\gamma K}. \tag{1.3}$$

Then any solution of (1.1) *with* (1.2) *satisfies* $\lim_{t\to\infty}(S(t), P(t)) = (\gamma, 0)$.

However, there is one question was left unsolved: Under which conditions will the susceptible bacteria $S(t)$ and viruses $P(t)$ coexist permanently?

In this work, we will study the permanence and extinction of system (1.1). To get the permanence, we engage Hale and Waltmann's persistence theory ([8]; for it applications, we refer the reader to Thieme [17,18] and Magal and Zhao [16], Liu et al. [10,19,15]). We also use similar techniques for global stability of stage-structured models (see Aiello et al. [1], Al-Omari et al. [2], Gourley and Kuang [6], Liu et al. [10–14,19,15], Beretta et al. [5] and Kuang [9]). We improve Theorem 1 by obtaining the necessary and sufficient conditions for extinction and permanence of system (1.1). Our main results are as follows:

Theorem 2. *System* (1.1) *with* (1.2) *is permanent if and only if it satisfies*

$$be^{-\mu_i T} > 1 + \frac{\mu_p}{\gamma K}. \tag{1.4}$$

Theorem 3. *The axis equilibrium* $(\gamma, 0)$ *of system* (1.1) *with* (1.2) *is globally attractive if and only if* (1.3) *holds.*

Remark 1. Theorem 3 suggests that (1.3) is also the necessary condition for extinction of viruses $P(t)$; this directly improves Theorem 1 in Gourley and Kuang [7].

Remark 2. By (3.2) in [7], the positive equilibrium of system (1.1) exists if and only if (1.4) holds true. Thus by Theorem 2, the permanence of (1.1) is equivalent to the existence of its positive equilibrium. The biological meanings from conditions (1.4) and (1.3) are: if and only if the difference of the recruitment rate of the virus and its leaving rate (by infecting bacteria) at the peak of bacterial abundance γ is larger than its death rate μ_p, then the viruses coexist with susceptible bacteria permanently; if the contrary, then the viruses face extinction.

2. Proof of main results

To prove the above main results, we need some preliminary results. We have

Lemma 1 (*Gourley and Kuang, [7], Proposition 1*). *Solutions of* (1.1) *with* (1.2) *satisfy* $S(t) > 0$, $P(t) > 0$ *for all* $t > 0$.

Lemma 2 (*Liu et al. [14], Lemma 2*). *For equation*

$$\dot{x}(t) = bx(t-\tau) - a_1 x(t) - a_2 x^2(t), \quad (a_1 \geq 0, a_2, b, \tau > 0 \text{ and } x(t) > 0 \text{ for all } -\tau \leq t \leq 0),$$

we have

(i) *If* $b > a_1$, *then* $\lim_{t\to+\infty} x(t) = \frac{b-a_1}{a_2}$.
(ii) *If* $b < a_1$, *then* $\lim_{t\to+\infty} x(t) = 0$.

To prove Theorem 2, we present the persistence theory of Hale and Waltmann [8] for infinite dimensional systems as follows.

Consider a metric space X with metric d. T is a continuous semiflow on X_1, i.e., a continuous mapping $T : [0, \infty) \times X \to X$ with the following properties:

$$T_t \circ T_s = T_{t+s}, \quad t, s \geq 0; \qquad T_0(x) = x, \quad x \in X.$$

Here T_t denotes the mapping from X to X given by $T_t(x) = T(t, x)$. The distance $d(x, y)$ of a point $x \in X$ from a subset Y of X is defined by

$$d(x, y) = \inf_{y \in Y} d(x, y).$$

Recall that the positive orbit $\gamma^+(x)$ through x is defined as $\gamma^+(x) = \bigcup_{t\geq 0}\{T(t)x\}$, and its ω-limit set is $\omega(x) = \bigcap_{T\geq 0} \mathrm{CL} \bigcup_{t\geq T}\{T(t)x\}$, where CL means the closure.

Define $W^s(A)$ the stable set of a compact invariant set A as

$$W^s(A) = \{x : x \in X, \omega(x) \neq \phi, \omega(x) \subset A\};$$

Define $\widetilde{A_\partial}$, the particular invariant sets of interest, as $\widetilde{A_\partial} = \bigcup_{x\in A_\partial} \omega(x)$, where A_∂ is the boundary of A.

(H_1) Assume X is the closure of open set X^0; ∂X^0 is nonempty and is the boundary of X^0. Moreover the C^0-semigroup $T(t)$ on X satisfies

$$T(t) : X^0 \to X^0, \quad T(t) : \partial X^0 \to \partial X^0.$$

Lemma 3 (*Hale and Waltman [8], Theorem 4.1, pp. 392*). *Suppose $T(t)$ satisfies* (H_1) *and:*

(i) *There is a $t_0 \geq 0$ such that $T(t)$ is compact for $t > t_0$.*
(ii) *$T(t)$ is point dissipative in X.*
(iii) *$\widetilde{A_\partial}$ is isolated and has an acyclic covering M.*

Then $T(t)$ is uniformly persistent if and only if for each $M_i \in M$, $W^s(M_i) \bigcap X^0 = \phi$.

Proof of Theorem 2. First we verify that the boundary planes of $R^2_+ = \{(S, P) : S \geq 0, P \geq 0\}$ repel the positive solutions to system (1.1) uniformly.

Let $C^+([-T, 0], R^2_+)$ denote the space of continuous functions mapping $[-T, 0]$ into R^2_+. We choose

$$C_1 = \{(\varphi_0, \varphi_1) \in C^+([-T, 0], R^2_+) : \varphi_0(\theta) \equiv 0, \theta \in [-T, 0]\},$$
$$C_2 = \{(\varphi_0, \varphi_1) \in C^+([-T, 0], R^2_+) : \varphi_0(\theta) > 0, \varphi_1(\theta) \equiv 0, \theta \in [-T, 0]\}.$$

Define $C = C_1 \bigcup C_2$, $X = C^+([-T, 0], R^2_+)$ and $X^0 = \mathrm{Int}\, C^+([-T, 0], R^2_+)$; then $C = \partial X^0$. It is easy to see that system (1.1) possesses two constant solutions in $C = \partial X^0$: $\widetilde{E_0} \in C_1$, $\widetilde{E_1} \in C_2$ with

$$\widetilde{E_0} = \{(\varphi_0, \varphi_1) \in C^+([-T, 0], R^2_+) : \varphi_0(\theta) \equiv \varphi_1(\theta) \equiv 0, \theta \in [-T, 0]\},$$
$$\widetilde{E_1} = \{(\varphi_0, \varphi_1) \in C^+([-T, 0], R^2_+) : \varphi_0(\theta) \equiv \gamma, \varphi_1(\theta) \equiv 0, \theta \in [-T, 0]\}.$$

We verify below that the conditions of Lemma 3 are satisfied. By the definition of X^0 and ∂X^0 and system (1.1), it is easy to see X^0 and ∂X^0 are invariant, and hence (H_1) is satisfied; conditions (i) and (ii) of Lemma 3 are clearly satisfied. Consider condition (iii) of Lemma 3; we have

$$\dot{S}(t)|_{(\varphi_0,\varphi_1)\in C_1} \equiv 0,$$

and thus $S(t)|_{(\varphi_0,\varphi_1)\in C_1} \equiv 0$ for all $t \geq 0$. Hence we have

$$\dot{P}(t)|_{(\varphi_0,\varphi_1)\in C_1} = -\mu_p P(t) - m P^2(t) \leq 0,$$

and then all points in C_1 approach $\widetilde{E_0} = (0, 0)$, i.e., $C_1 = W^s(\widetilde{E_0})$. On the other hand, we have $\dot{P}(t)|_{(\varphi_0,\varphi_1)\in C_1} \equiv 0$, and thus $P(t)|_{(\varphi_0,\varphi_1)\in C_1} \equiv 0$ for all $t \geq 0$. Then we have

$$\dot{S}(t)|_{(\varphi_0,\varphi_1)\in C_2} = \alpha S(t)\left(1 - \frac{S(t)}{\gamma}\right),$$

and it follows that $\lim_{t\to\infty} S(t) = \gamma$. Thus all points in C_2 approach $\widetilde{E_1}$, i.e., $C_2 = W^s(\widetilde{E_1})$. Hence $\widetilde{A_\partial} = \widetilde{E_0} \bigcup \widetilde{E_1}$ and clearly it is isolated. Noting that $C_1 \bigcap C_2 = \phi$, it follows from these structural features that the flow in $\widetilde{A_\partial}$ is acyclic. Since $\widetilde{A_\partial}$ has a covering $M = \widetilde{A_\partial} = \widetilde{E_0} \bigcup \widetilde{E_1}$, which, as proved above, is acyclic, this satisfies condition (iii) of Lemma 3.

Now we show that $W^s(\widetilde{E}_i)\bigcap X^0 = \phi, i = 0, 1$. Since Lemma 1 indicates $W^s(\widetilde{E}_0)\bigcap X^0 = \phi$, we only need to verify $W^s(\widetilde{E}_1)\bigcap X^0 = \phi$. Assume it is false, i.e., $W^s(\widetilde{E}_1)\bigcap X^0 \neq \phi$; then there must exist a positive solution $(S(t), P(t))$ to system (1.1) such that $\lim_{t\to\infty}(S(t), P(t)) = (\gamma, 0)$. Then for the sufficiently small ε with

$$\varepsilon < \frac{1}{2(1+m)} \cdot \frac{K\gamma(b\mathrm{e}^{-\mu_i T} - 1) - \mu_p}{K(b\mathrm{e}^{-\mu_i T} + 1)},$$

there exists a positive constant $T_0 = T_0(\varepsilon)$ such that

$$\gamma + \varepsilon > S(t) > \gamma - \varepsilon > 0, \quad P(t) < \varepsilon \quad \text{for all } t \geq T_0.$$

Then it follows from the second equation of (1.1) that

$$P'(t) > bK(\gamma - \varepsilon)\mathrm{e}^{-\mu_i T}P(t - T) - \mu_p P(t) - K(\gamma + \varepsilon)P(t) - mP^2(t), \quad t \geq T_0 + T. \tag{2.5}$$

Consider the delay differential equation

$$\begin{cases} v'(t) = bK(\gamma - \varepsilon)\mathrm{e}^{-\mu_i T}v(t - T) - [K(\gamma + \varepsilon) + \mu_p]v(t) - mv^2(t), \quad t \geq T_0 + T, \\ v(t) \equiv P(t), \quad t \in [T_0, T_0 + T]. \end{cases} \tag{2.6}$$

By (2.5) and the comparison theorem, we have $P(t) \geq v(t)$ for all $t > T_0$. On the other hand by Lemma 2, we have $\lim_{t\to\infty} v(t) = v^*$ for all solutions to system (2.6), where

$$v^* = \frac{1}{m} \cdot \left\{ bK(\gamma - \varepsilon)\mathrm{e}^{-\mu_i T} - [K(\gamma + \varepsilon) + \mu_p] \right\} > \varepsilon$$

is the unique positive equilibrium of system (2.6). Then we get $\lim_{t\to\infty} P(t) \geq v^*$, a contradiction to $P(t) < \varepsilon$ for all $t \geq T_0$. Hence condition $W^s(\widetilde{E}_i)\bigcap X^0 = \phi, i = 0, 1$ of Lemma 3 must hold true.

Thus we get that system (1.1) satisfies all conditions for Lemma 3, so we have that $(S(t), P(t))$ is uniformly persistent, i.e., there exist positive constants ϵ and $T_1 = T_1(\epsilon)$ such that $S(t), P(t) \geq \epsilon$ for all $t \geq T_1$. Furthermore, following arguments similar to those of Lemma 2.5 (Beretta and Kuang [4], 2001) we can prove that (S, P) is ultimately bounded, i.e., system (1.1) is dissipative, and this proves the permanence of system (1.1).

We verify below that from the permanence of system (1.1) it follows that (1.4) holds. Assume this is false, i.e., $b\mathrm{e}^{-\mu_i T} \leq 1 + \frac{\mu_p}{\gamma K}$; by Theorem 1, we get $\lim_{t\to\infty}(S(t), P(t)) = (\gamma, 0)$, a contradiction to the permanence of system (1.1). Thus (1.4) must hold true. This proves Theorem 2. ■

Proof of Theorem 3. By Theorem 1, we have that $(\gamma, 0)$ is globally attractive provided that (1.3) holds. Given the global attractability of $(\gamma, 0)$, we claim that (1.3) must hold; otherwise if the contrary holds, we have $b\mathrm{e}^{-\mu_i T} > 1 + \frac{\mu_p}{\gamma K}$. Thus from Theorem 2, system (1.1) will be permanent. Hence we get a contradiction to the global attractability of $(\gamma, 0)$. Then (1.3) must hold; this proves Theorem 3. ■

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